WINTER ECOLOGY OF THE PORCUPINE, *Erethizon dorsatum*

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This thesis submitted by Cheryl Tenneson in partial fulfillment of the requirements for the Degree of Masters of Science from the University of North Dakota is hereby approved by the Faculty Advisory Committee under whom the work has been done.

Travis W. Reynolds

Richard W. Caldwell

John C. LaPoint

This thesis meets the standards for appearance and conforms to the style and format requirements of the Graduate School of the University of North Dakota, and is hereby approved.

Title WINTER ECOLOGY OF THE PORCUPINE, *Erethizon dorsatum*

Department Biology

Degree Master of Science

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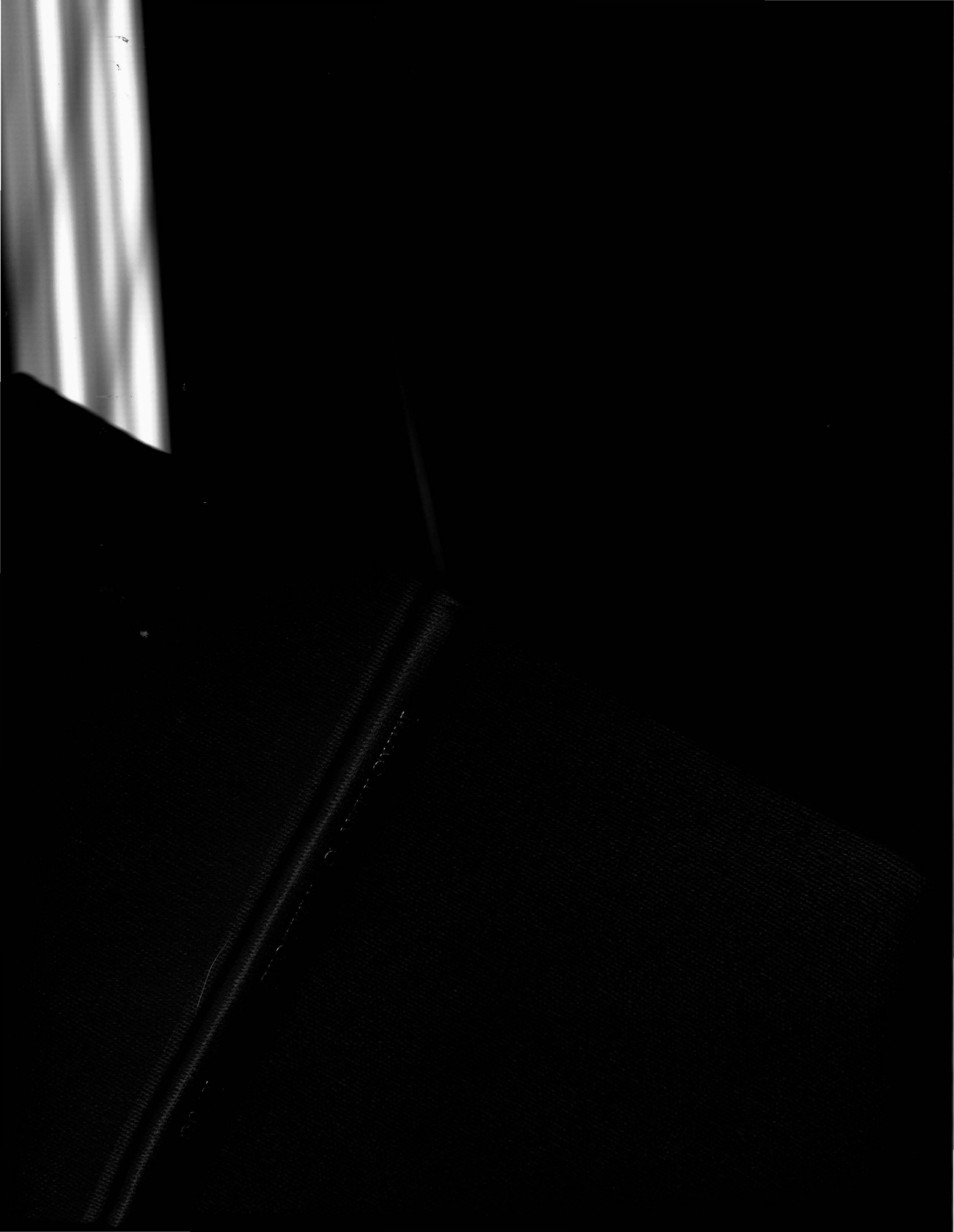

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ABSTRACT

During the winter of 1982 a study of porcupine behavioral ecology was conducted at Lake Itasca State Park in northwestern Minnesota. Daily observations were made on 15 individually marked porcupines. Data were taken on porcupine locations, positions, and activities. In addition, weather and habitat data were collected. Porcupines utilized behavioral means of thermoregulation such as positioning themselves low in the trees for shelter, and feeding and keeping active at low ambient temperatures to increase heat production. Dens were rarely used and then only when ambient temperatures dropped below -9°C. Two groups of porcupines were studied in depth. Each group consisted of one adult male, and several females and juveniles. It was postulated that these were family groups. An extensive habitat analysis was conducted during the summer of 1982. The most important aspects of desirable winter home ranges were relatively high proportions of larger diameter trees and presence of white pine (Pinus strobus). Tree density was not an important factor. White pine was utilized more than any other species. It was used

for food (bark and needles) and as a resting place. Porcupines are not the principal threat to white pine in Itasca State Park. The pines are relatively scarce and are mostly overmature. Hence, forest management should concentrate on maximizing white pine reproduction and control measures should be aimed primarily at animals that harm the seed crop and seedlings.

INTRODUCTION

The porcupine (Erethizon dorsatum), a member of the family Erethizontidae, is found in the northern lake states, northeastern and western United States, Alaska, and most of Canada, in a wide variety of environments ranging from desert-shrub (Reynolds 1957) to tundra (Murie 1926). It is unique among North American rodents in its use of spines for defense and its litter size of one.

Porcupine foraging behavior is important to investigate from a forest management point of view. Winter feeding on the inner cambium layer can cause permanent damage and death of trees (Gabrielson 1928; Ludeman 1954; Storm and Halvorson 1967). Most previous work on porcupine foraging behavior has concerned feeding methods (e.g. girdling and limbing) and food preferences. Food preference appears to vary between and within populations (Marshall et al. 1962). Factors implicated in the determination of food preferences and tree choice include food availability (Speer and Dilworth 1978), season (Gabrielson 1928; Brander 1973), tree density (Curtis and Wilson 1953; Harder 1980), tree diameter (Krefting et al. 1962; Marshall et al. 1962; Rudolf 1949; Van Deusen and Myers 1962), and insulation cover (Clarke and Brander 1973). No single study has addressed the

interaction of the above factors in determining food preference and tree choice.

Two aspects of porcupine behavior that have not been studied extensively are movements and social behavior in the wild, particularly in winter. The most intensive study of home range size and daily movements was conducted by Smith (1979). He used radio-telemetry to track six porcupines from November through August in northeastern Oregon. Faulkner and Dodge (1962) briefly discussed summer and winter home ranges although specific data and sample sizes were not included.

Most investigations of porcupine reproductive and social behavior were based upon captives (Struthers 1928, Shadle 1946; Shadle 1951; Shadle 1954). Observations of reproductive and social behavior in the wild are limited to a few brief descriptive accounts (Gabrielson 1928; Struthers 1928; Spencer 1950; Brander 1973). There are no published accounts of winter social behavior other than communal denning (Faulkner and Dodge 1962).

Porcupines are active year round in regions where winter temperatures frequently fall below -15°C. Irving et al. (1955) reported a lower critical temperature of -12°C for porcupines in winter in Alaska. In order to maintain a constant body temperature at ambient temperatures below the lower critical temperature, an animal must

increase its metabolic rate to produce heat, and this requires energy. Porcupines living in regions with harsh winters might be expected to utilize some means of behavioral thermoregulation in order to minimize thermal stress. Clarke and Brander (1973) demonstrated nocturnal behavioral thermoregulation in porcupines in Massachusetts. Porcupines chose hemlock (Tsuga canadensis) cover to minimize radiant heat loss. Diurnal behavioral thermoregulation of porcupines in the wild has not been reported.

From January-August 1982, I conducted a study of porcupines at Itasca State Park in northwestern Minnesota with the goal of determining 1) winter food and habitat preferences, 2) extent of bark damage inflicted by porcupines, 3) winter movements and home range sizes, 4) degree of winter social interactions, and 5) the effect of the thermal environment on behavior.

MATERIALS AND METHODS

Porcupines located on the ground were picked up by the tail and placed in a hogwire handling cone similar to that of Shadle (1950). Animals in trees were caught in a funnel trap at the tree base. This trap consisted of a 1.2-1.5 m chicken wire fence surrounding the trunk of the tree, with an opening where a wire box treadle trap (28 X 30 X 79 cm) was placed.

Animals were weighed with a portable spring scale (Sunbeam Stewart, cat no 8020). Porcupines were permanently eartagged (National Band and Tag Co self piercing tag, style 4-1005, size 3). Individual identification in trees was not possible using ear tags alone. Therefore, each animal was sprayed with enamel paint on the hindquarters. Paint remained visible for approximately two months. Animals were classified as juveniles (born the previous spring) or adults on the basis of coat color (Woods 1973) and size. Juveniles were darker than adults and weighed less than 4.5 kg.

Observations were made from 19 January through 12 April 1982 at seven study sites within Itasca State Park (Figure 1). Data were recorded on the following parameters: individual identification, time of day, location, height

above ground, distance from trunk, branch diameter (estimated), direction faced, direction of trunk relative to animal, activity, and feeding. Porcupine height was measured using an clinimeter (Haga, West Germany). Feeding activities were broken down into the following classes: feeding on needles, feeding on bark of trunk and/or branches, feeding on bark of twigs, feeding on bark of twigs and bark trunk and/or branches, feeding on buds, feeding on bark of twigs and buds, and not feeding. Each animal was monitored for about 15 minutes while measurements were recorded.

Trees used by porcupines were marked with numbered metal tags and the following data were recorded: species, dbh (diameter at breast height), height, height of lowest branch, and dbh of other stems. The positions of the trees utilized by the porcupines were mapped using a compass, rangefinder (Ranging Measuring System model 600), and a 15 m tape. Home range areas were calculated using the minimum polygon method (Mohr 1947) that connects outermost observation points to form home range boundaries.

Weather data were generally recorded daily. A maximum/minimum thermometer (Springfield) was fixed to the north side of a tree near each porcupine's den (if the porcupine lacked a den, the thermometer was fixed to a tree near the center of the animal's home range). Daily weather

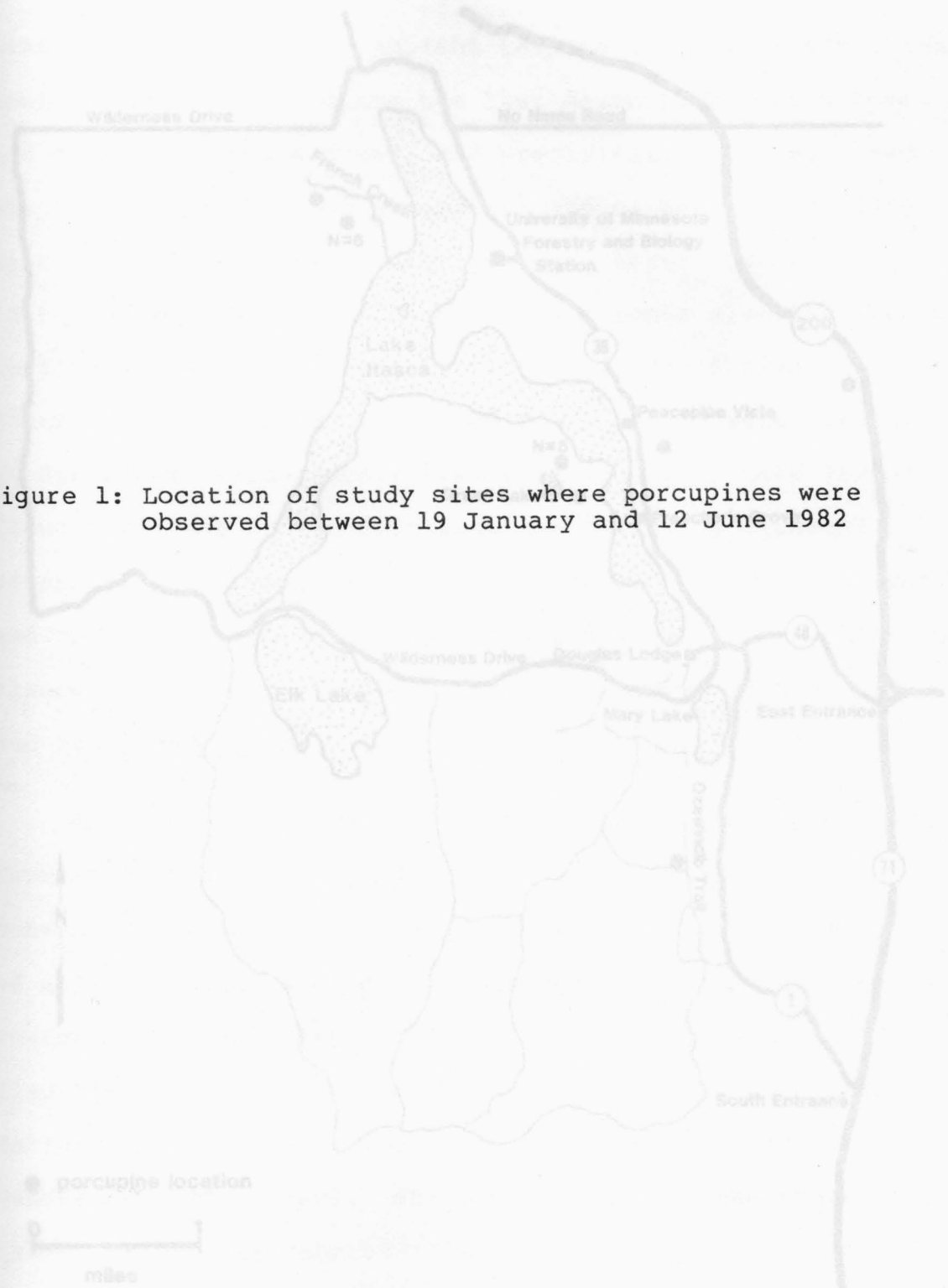
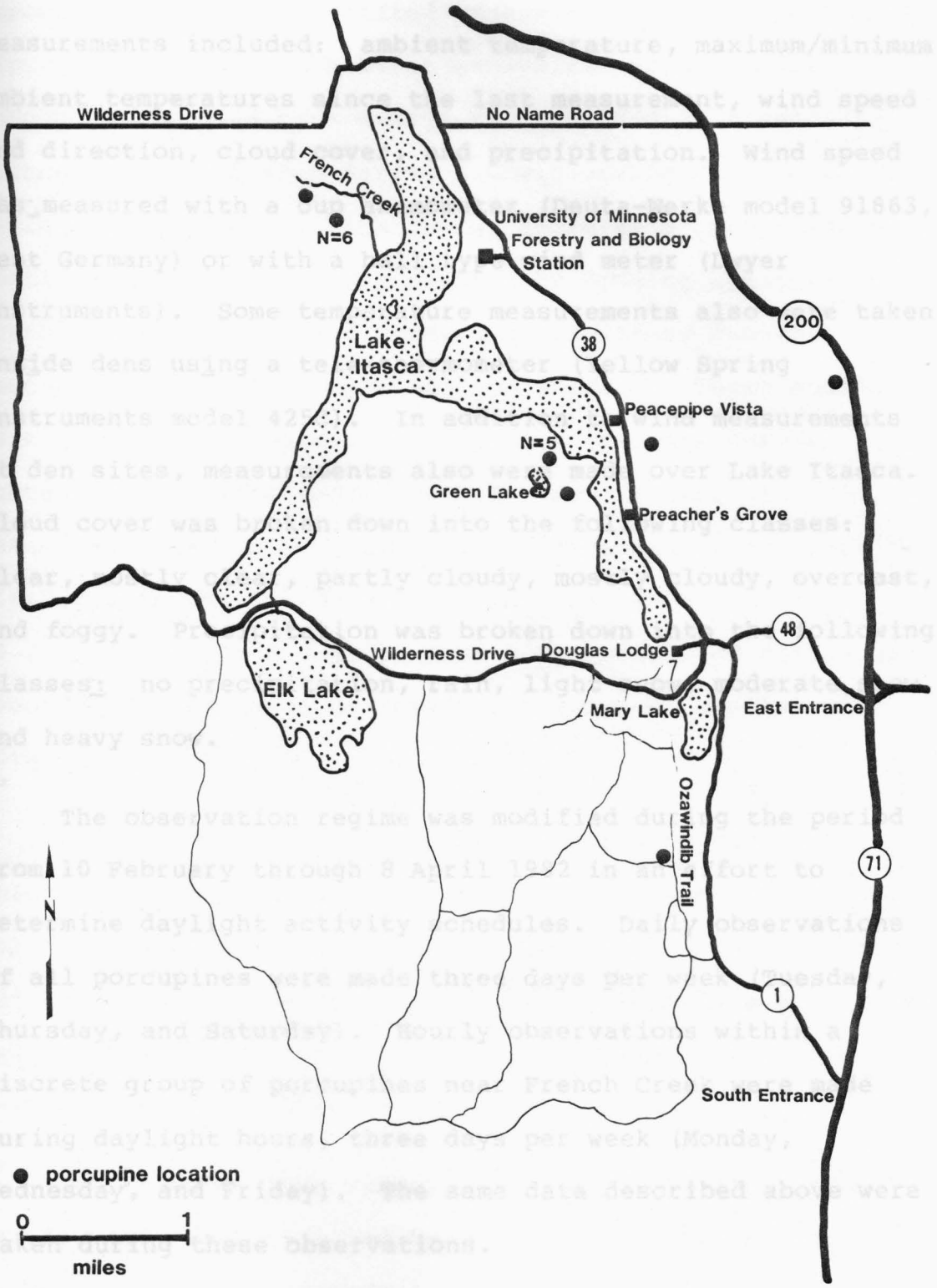


Figure 1: Location of study sites where porcupines were observed between 19 January and 12 June 1982


Wilderness Drive
No Name Road
French Creek
N=6
University of Minnesota
Forestry and Biology
Station
200
38
Lake
Itasca
Peacepipe Vista
N=5
Green Lake
Preacher's Grove
48
Wilderness Drive
Douglas Lodge
Elk Lake
Mary Lake
East Entrance
Ozawindib Trail
71
1
South Entrance
N
porcupine location
0
1
miles

measurements included: ambient temperature, maximum/minimum ambient temperatures since the last measurement, wind speed and direction, cloud cover, and precipitation. Wind speed was measured with a cup anemometer (Deuta-Werke model 91863, West Germany) or with a ball type wind meter (Dwyer Instruments). Some temperature measurements also were taken inside dens using a tele-thermometer (Yellow Spring Instruments model 425C). In addition to wind measurements at den sites, measurements also were made over Lake Itasca. Cloud cover was broken down into the following classes: clear, mostly clear, partly cloudy, mostly cloudy, overcast, and foggy. Precipitation was broken down into the following classes: no precipitation, rain, light snow, moderate snow, and heavy snow.

The observation regime was modified during the period from 10 February through 8 April 1982 in an effort to determine daylight activity schedules. Daily observations of all porcupines were made three days per week (Tuesday, Thursday, and Saturday). Hourly observations within a discrete group of porcupines near French Creek were made during daylight hours, three days per week (Monday, Wednesday, and Friday). The same data described above were taken during these observations.

With the melting of snow, depended upon to track porcupines, the study shifted emphasis from behavior to tree damage assessment and habitat analysis. From 16 April through 8 May 1982 bark damage was assessed in trees porcupines had visited during the winter. Each tree was assigned a subjective bark damage score as a percentage of total bark. This was accomplished by drawing hypothetical trees on graph paper and shading in arbitrary cutoff percentages (5%, 10%, 25%, 50%) of surface. These models were then used as guides to determine the bark damage scores. Trees were scored both for new (winter of 1981-1982) and old bark damage. Bark damage scores were divided into the following classes: 0%, 1-5%, 6-10%, 11-25%, 26-50%, and greater than 50%. Height of damage was recorded and evidence of feeding on twigs or needles was noted.

From 10 May through 3 August 1982 I conducted an extensive habitat analysis. Within winter home ranges the following data were taken on all trees over 3.3 cm dbh (this was the smallest dbh observed to be utilized by a porcupine during this study): species, dbh, and presence/absence of new and old bark damage.

Two types of home ranges were analyzed: actual home ranges which were utilized by porcupines and sham home ranges which were artificially constructed for comparative

purposes. Actual home ranges were further broken down into two categories: early winter home ranges and the larger late winter home ranges. Habitat analysis of the actual porcupine home ranges consisted of sampling all of the plots within early winter home ranges and 5% of the plots (randomly chosen) within the extensive late winter home ranges.

Eight sham home ranges were constructed by randomly choosing actual porcupine early winter home ranges and creating sham areas identical in size and shape to them. Four sham home ranges were randomly interspersed among actual home ranges at French Creek and four others were similarly placed at Green Lake to compare utilized and unutilized areas.

Statistical tools used to analyse the data included: G-test, point biserial correlation coefficient, Pearson's correlation coefficient, principal components analysis, t-test, and analysis of variance. A statistical programming package, Statistical Analysis System (SAS Institute Inc.), was used for most of the analyses performed.

RESULTS

Observations were made on 17 porcupines, 14 of which were captured, marked, sexed, and weighed. Of the 14 captured animals, 11 occurred in two discrete groups: five animals (four females and one male) near Green Lake on the peninsula between the east and west arms of Lake Itasca, and six animals (four females and two males) on the peninsula southwest of French Creek. Of the animals captured, females outnumbered males nine to five.

FOOD AND HABITAT PREFERENCES

Composition of tree species in actual home ranges was compared between two groups of porcupines (French Creek and Green Lake) (Table 1). Sham home ranges were also compared with actual home ranges relative to tree species composition. Tree species composition varied significantly between French Creek and Green Lake actual home ranges. The predominant overstory species at French Creek included American basswood, balsam fir, paper birch, white pine, and American elm. The predominant overstory species at Green Lake included paper birch, quaking aspen, red maple, American basswood, and red oak. There was a much greater abundance and diversity of conifers at French Creek than at

Green Lake, although the overall species diversity at Green Lake (17 species) was richer than at French Creek (12 species).

Tree species composition varied significantly between actual and sham home ranges at French Creek and at Green Lake. White pine was less abundant in sham home ranges at both sites. At Green Lake, paper birch and red maple were also less abundant in sham home ranges, and red oak and sugar maple were more abundant. Species diversity was slightly greater in French Creek sham home ranges and slightly less in Green Lake sham home ranges.

Tree size distribution in actual home ranges was compared for French Creek and Green Lake (Table 2). Sham home ranges were also compared with actual home ranges relative to dbh composition. Tree dbh distribution varied significantly between French Creek and Green Lake actual home ranges. There was a greater proportion of smaller stems (<14.9 cm) and medium stems (37.5-67.4 cm) at French Creek. There was a greater proportion of moderately small stems (15.0-37.4 cm) and large stems (67.5 cm and greater) at Green Lake.

Tree size distribution in sham home ranges was significantly different than that of actual home ranges at French Creek. There was a greater proportion of very small stems (<7.4 cm); and moderate sized stems (30.0-67.4 cm)

TABLE 1

Tree species frequency by study site

Species	Study site: French Creek, Actual home range N	French Creek, Actual home range %	French Creek, Sham home range N	French Creek, Sham home range %	Green Lake, Actual home range N	Green Lake, Actual home range %	Green Lake, Sham home range N	Green Lake, Sham home range %
White pine (Pinus strobus)	38	6.7	10	1.4	12	1.1	1	0.2
Red oak (Quercus rubra)	0	0	0	0	32	3.0	61	9.7
White spruce (Picea glauca)	7	1.2	9	1.2	9	0.9	0	0
Quaking aspen (Populus tremuloides)	0	0	0	0	111	10.5	65	10.4
Bigtooth aspen (Populus grandidentata)	0	0	0	0	5	0.5	4	0.6
Balsam fir (Abies balsamea)	62	10.9	95	12.9	9	0.9	0	0
American elm (Ulmus americana)	33	5.8	66	9.0	8	0.8	0	0
Bur oak (Quercus macrocarpa)	0	0	5	0.7	23	2.2	4	0.6
Sugar maple (Acer saccharum)	0	0	0	0	25	2.4	49	7.8
American basswood (Tilia americana)	70	12.3	110	15.0	91	8.6	32	5.1
Red pine (Pinus resinosa)	9	1.6	2	0.3	7	0.7	0	0
Ash (Fraxinus sp.)	112	19.6	304	41.4	56	5.3	10	1.6
Paper birch (Betula papyrifera)	58	10.2	50	6.8	281	26.6	62	9.9
Mountain maple (Acer spicatum)	143	25.0	61	8.3	3	0.3	0	0
Prunus sp.	35	6.1	13	1.8	5	0.5	3	0.5
Amelanchier sp.	1	0.2	0	0	0	0	0	0
Black spruce (Picea mariana)	3	0.5	4	0.5	0	0	0	0
Ironwood (Ostrya virginiana)	0	0	2	0.3	279	26.4	317	50.6
Red maple (Acer rubrum)	0	0	1	0.1	99	9.4	15	2.4
Hazelnut (Corylus sp.)	0	0	2	0.3	0	0	2	0.3
Jack pine (Pinus banksiana)	0	0	0	0	0	0	1	0.2
Total	571	100.1	734	100.0	1055	100.1	626	99.9

Actual home range by study site significantly different ($p<0.0001$; $G=1122.948$; $df=20$).
Sham home ranges significantly different from actual home ranges at French Creek ($p<0.0001$; $G=103.602$; $df=25$) and at Green Lake ($p<0.0001$; $G=289.48$; $df=25$).

TABLE 2

Tree dbh frequencies by study site

DBH (cm)	Study site: French Creek Actual home range N	French Creek Actual home range %	French Creek Sham home range N	French Creek Sham home range %	Green Lake Actual home range N	Green Lake Actual home range %	Green Lake Sham home range N	Green Lake Sham home range %
<7.4	326	56.5	514	68.5	502	46.7	321	50.3
7.5-14.9	124	21.5	152	20.3	218	20.3	148	23.2
15.0-22.4	28	4.9	21	2.8	190	17.7	65	10.2
22.5-29.9	26	4.5	17	2.3	94	8.8	65	10.2
30.0-37.4	21	3.6	19	2.5	42	3.9	31	4.9
37.5-44.9	18	3.1	20	2.7	12	1.1	7	1.1
45.0-52.4	13	2.3	3	0.4	3	0.3	0	0
52.5-59.9	14	2.4	2	0.3	1	0.1	0	0
60.0-67.4	3	0.5	2	0.3	1	0.1	0	0
67.5-74.9	2	0.3	0	0	6	0.6	0	0
75.0-82.4	1	0.2	0	0	3	0.3	0	0
82.5-89.9	1	0.2	0	0	2	0.2	0	0
>90.0	0	0	0	0	0	0	1	0.2
Total	577	100.0	750	100.1	1074	100.1	638	100.1

Actual home range dbh compositions by study site significantly different ($p<0.001$; $G=165.31$; $df=12$).

Sham home range dbh compositions significantly different from actual home ranges at French Creek ($p<0.001$; $G=48.382$; $df=12$) and at Green Lake ($p<0.001$; $G=37.23$; $df=12$).

were less abundant. There were no large stems (67.5 cm and greater) in French Creek sham home ranges. Tree size distribution in sham home ranges was significantly different than that of actual home ranges at Green Lake. There was a greater proportion of small stems (<14.9 cm); and moderate to large stems (45.0 cm and greater) were completely absent in Green Lake sham home ranges.

The mean tree density at French Creek was 5.74 trees/100 m^2 for actual home ranges and 5.71 trees/100 m^2 for sham home ranges. The mean tree density at Green Lake was 5.45 trees/100 m^2 for actual home ranges and 5.48 trees/100 m^2 for sham home ranges. Tree densities were comparable between study sites and between sham and actual home ranges.

Tree species with new bark damage differed significantly from total tree species present at French Creek (Table 3). Porcupines preferred white pine, American elm, and American basswood based on what was available to them. White pine was preferred most, with 65.8% of the available trees sustaining new bark damage. Tree species sustaining the most extensive individual damage were white pine and American basswood.

Tree species with new bark damage differed significantly from tree species available at Green Lake (Table 4). Porcupines preferred (in order of priority) white pine, bigtooth aspen, and red oak based on availability. Tree species sustaining the most extensive individual tree damage were red oak, white pine, and bigtooth aspen. Red oaks seemed particularly sensitive to extensive damage and leafing out of damaged limbs was retarded or entirely prevented.

TABLE 3

Observation frequencies by new bark damage score and species for French Creek

Species	Total present			Number damaged		New bark damage score (%)				
	N	%	%Damaged	N	%	1-5	6-10	11-25	26-50	50
White pine	38	6.7	65.8	25	50.0	18	5	1	1	0
White spruce	7	1.2	14.3	1	2.0	1	0	0	0	0
Balsam fir	62	10.9	6.5	4	8.0	4	0	0	0	0
American elm	33	5.8	30.3	10	20.0	10	0	0	0	0
American basswood	70	12.3	14.3	10	20.0	7	3	0	0	0
Red pine	9	1.6	0	0	0	0	0	0	0	0
Ash	112	19.6	0	0	0	0	0	0	0	0
Paper birch	58	10.2	0	0	0	0	0	0	0	0
Mountain maple	143	25.0	0	0	0	0	0	0	0	0
Prunus sp.	35	6.1	0	0	0	0	0	0	0	0
Amelanchier sp.	1	0.2	0	0	0	0	0	0	0	0
Black spruce	3	0.5	0	0	0	0	0	0	0	0
Total	571	100.1	-	50	100.0	40	8	1	1	0

New bark damage significantly related to tree species ($p<0.0001$; $G=122.03$; $df=11$).

New bark damage score frequencies by dbh class for French Creek are summarized in Table 5. The mean dbh of damaged trees at French Creek was 40.6 cm and the mean dbh of all trees was 13.0 cm. Classes of dbh with new bark damage differed significantly from dbh classes present at French Creek. Porcupines preferred trees greater than 15.0 cm in diameter, and generally preference increased with increasing dbh.

New bark damage was significantly related to dbh class at Green Lake (Table 6). The mean dbh of damaged trees was 33.0 cm and the mean dbh of all trees was 12.7 cm at Green Lake. Porcupines preferred trees greater than 30.0 cm in diameter. No trees 52.5-67.4 cm in diameter were damaged, presumably because of their very low frequencies of occurrence (0.1%). The most preferred sizes were 30.0-52.4 cm and 75.0-89.9 cm.

In addition to investigating tree preference on the basis of new bark damage, the frequency of direct observations of porcupines in trees was considered. Green Lake porcupines utilized a wider variety of species than French Creek porcupines (Table 7). The following species had observation frequencies greater than 5% (ranked by decreasing utilization frequency): white pine, red oak, American basswood, and bigtooth aspen. French Creek

TABLE 4

Observation frequencies by new bark damage score and tree species for Green Lake

Species	Total present			Number damaged		New bark damage score (%)				
	N	%	%Damaged	N	%	1-5	6-10	11-25	26-50	50
White pine	12	1.1	41.7	5	18.5	4	1	0	0	0
Red oak	32	3.0	34.4	11	40.7	6	0	3	1	1
White spruce	9	0.8	0	0	0	0	0	0	0	0
Quaking aspen	121	11.4	3.3	4	14.8	4	0	0	0	0
Bigtooth aspen	5	0.5	40.0	2	7.4	1	1	0	0	0
Balsam fir	9	0.8	0	0	0	0	0	0	0	0
American elm	8	0.8	0	0	0	0	0	0	0	0
Bur oak	23	2.2	8.7	2	7.4	2	0	0	0	0
Sugar maple	25	2.3	8.0	2	7.4	2	0	0	0	0
American basswood	91	8.5	1.1	1	3.7	1	0	0	0	0
Red pine	7	0.7	0	0	0	0	0	0	0	0
Ash	56	5.3	0	0	0	0	0	0	0	0
Paper birch	281	26.4	0	0	0	0	0	0	0	0
Mountain maple	3	0.3	0	0	0	0	0	0	0	0
Prunus sp.	5	0.5	0	0	0	0	0	0	0	0
Ironwood	279	26.2	0	0	0	0	0	0	0	0
Red maple	99	9.3	0	0	0	0	0	0	0	0
Total	1065	100.1	-	27	99.9	20	2	3	1	1

New bark damage significantly related to tree species ($p<0.0001$; $G=811.066$; $df=16$).

porcupines relied much more heavily on white pine than did Green Lake porcupines. Species with observation frequencies greater than 5% were (ranked by decreasing utilization frequency): white pine and American elm. Tree species utilization was significantly different between French Creek and Green Lake porcupines. Note that tree species utilization does not necessarily indicate feeding utilization. French Creek porcupines depended on needles for food more than bark, while the reverse was true for Green Lake porcupines (Table 8).

Tree species utilization and sex were significantly related in both porcupine groups (Table 9). French Creek females utilized less American elm and American basswood and more white spruce and balsam fir than males. Females also utilized conifers 6% more than males. Green Lake females utilized less red oak, white spruce, quaking aspen, and bur oak, and more white pine, bigtooth aspen, American basswood, and red pine than males. Females utilized conifers 17% more often than males. Porcupine sex and food type were not significantly related for either French Creek or Green Lake porcupines.

Porcupine age was significantly related to choice of trees foraged upon at both study sites (Table 10). White pine was utilized equally by French Creek juveniles and

TABLE 5

Observation frequencies by new bark damage score and dbh class for French Creek

DBH (cm)	Total present			Number damaged		New bark damage score (%)				
	N	%	%Damaged	N	%	1-5	6-10	11-25	26-50	50
7.4	326	56.5	0	0	0	0	0	0	0	0
7.5-14.9	124	21.5	0.8	1	2.0	0	1	0	0	0
15.0-22.4	28	4.9	32.1	9	18.0	8	1	0	0	0
22.5-29.9	26	4.5	15.4	4	8.0	4	0	0	0	0
30.0-37.4	21	3.6	42.9	9	18.0	8	1	0	0	0
37.5-44.9	18	3.1	55.6	10	20.0	7	3	0	0	0
45.0-52.4	13	2.3	46.2	6	12.0	4	2	0	0	0
52.5-59.9	14	2.4	42.9	6	12.0	6	0	0	0	0
60.0-67.4	3	0.5	66.7	2	4.0	1	0	1	0	0
67.5-74.9	2	0.3	50.0	1	2.0	1	0	0	0	0
75.0-82.4	1	0.2	100.0	1	2.0	1	0	0	0	0
82.5-89.9	1	0.2	100.0	1	2.0	0	0	0	1	0
90.0	0	0	0	0	0	0	0	0	0	0
Total	577	100.0	-	50	100.0	40	8	1	1	0

New bark damage significantly related to dbh class ($p<0.0001$; $G=130.804$; $df=12$).

adults. Juveniles utilized more balsam fir and American basswood than adults. Adults utilized more American elm and white spruce than juveniles, and juveniles utilized 8% more conifers than adults. Green Lake adults were utilizing white pine during 45% of the observations. Red oak, American basswood, and other hardwoods made up the remainder of the adult tree species utilization. One observation of red pine utilization was made. There was only a single juvenile monitored at Green Lake and it depended entirely on white pine.

TABLE 6

Observation frequencies by new bark damage score and dbh class for Green Lake

DBH (cm)	Total present			Number damaged		New bark damage score (%)				
	N	%	%Damaged	N	%	1-5	6-10	11-25	26-50	50
7.4	502	46.7	0.4	2	7.1	0	1	0	1	0
7.5-14.9	218	20.3	1.4	3	10.7	1	0	1	0	1
15.0-22.4	190	17.7	0.5	1	3.6	1	0	0	0	0
22.5-29.9	94	8.8	7.4	7	25.0	5	0	2	0	0
30.0-37.4	42	3.9	21.4	9	32.1	8	1	0	0	0
37.5-44.9	12	1.1	16.7	2	7.1	2	0	0	0	0
45.0-52.4	3	0.3	66.7	1	3.6	1	0	0	0	0
52.5-59.9	1	0.1	0	0	0	0	0	0	0	0
60.0-67.4	1	0.1	0	0	0	0	0	0	0	0
67.5-74.9	6	0.6	16.7	1	3.6	1	0	0	0	0
75.0-82.4	3	0.3	66.7	1	3.6	1	0	0	0	0
82.5-89.9	2	0.2	50.0	1	3.6	1	0	0	0	0
90.0	0	0	0	0	0	0	0	0	0	0
Total	1074	100.1	-	28	100.0	21	2	3	1	1

New bark damage significantly related to dbh class ($p<0.0001$; $G=62.144$; $df=12$).

TABLE 7

Frequencies of observations for each tree species by study site

Species	French Creek N	French Creek %	Green Lake N	Green Lake %
White pine	453	85.3	59	55.1
Red oak	0	0	16	15.0
White spruce	0	0	3	2.8
Quaking aspen	0	0	3	2.8
Bigtooth aspen	0	0	7	6.5
Balsam fir	19	3.6	1	0.9
American elm	44	8.3	1	0.9
Bur oak	0	0	1	0.9
American basswood	15	2.8	9	8.4
Red pine	0	0	3	2.8
Unidentified hardwood	0	0	4	3.7
Total	531	100.0	107	99.8

Tree species utilization significantly different between study sites ($p<0.001$; $G=160.658$; $df=10$).

TABLE 8

Frequencies of observations for each food type by study site

Food type	French Creek N	French Creek %	Green Lake N	Green Lake %
Bark and twigs	2	0.4	1	0.9
Bark	15	2.9	12	10.5
Twigs and buds	1	0.2	0	0.0
Needles	45	8.7	4	3.5
Not feeding	453	87.6	96	84.2
Twigs	1	0.2	1	0.9
Total	517	100.0	114	100.0

Food type choice significantly different for French Creek and Green Lake ($p<0.01$; $G=16.766$; $df=5$).

TABLE 9

Frequencies of observations for each tree species by porcupine sex and study site

Tree species	French Creek				Green Lake			
	Males		Females		Males		Females	
	N	%	N	%	N	%	N	%
White pine	75	83.3	322	83.0	12	38.7	44	62.0
Red oak	0	0	0	0	11	35.5	5	7.0
White spruce	0	0	3	0.8	3	9.7	0	0
Quaking aspen	0	0	0	0	2	6.5	1	1.4
Bigtooth aspen	0	0	0	0	2	6.5	5	7.0
Balsam fir	0	0	19	4.9	0	0	0	0
American elm	11	12.2	33	8.5	0	0	0	0
Bur oak	0	0	0	0	1	3.2	0	0
American basswood	4	4.4	11	2.8	0	0	9	12.7
Red pine	0	0	0	0	0	0	3	4.2
Unidentified hardwood	0	0	0	0	0	0	4	5.6
Total	90	99.9	388	100.0	31	100.1	71	99.9

Sex and tree species choice were significantly related at French Creek ($p<0.05$; $G=10.75$; $df=4$) and at Green Lake ($p<0.001$; $G=35.022$; $df=8$).

TABLE 10

Frequencies of observations for each tree species by porcupine age and study site

Tree species	French Creek				Green Lake			
	Juveniles		Adults		Juveniles		Adults	
	N	%	N	%	N	%	N	%
White pine	111	85.4	342	84.7	20	100.0	32	44.4
Red oak	0	0	0	0	0	0	16	22.2
White spruce	0	0	3	0.7	0	0	3	4.2
Quaking aspen	0	0	0	0	0	0	2	2.8
Bigtooth aspen	0	0	0	0	0	0	3	4.2
Balsam fir	12	9.2	7	1.7	0	0	1	1.4
American elm	1	0.8	43	10.6	0	0	0	0
Bur oak	0	0	0	0	0	0	1	1.4
American basswood	6	4.6	9	2.2	0	0	9	12.5
Red pine	0	0	0	0	0	0	1	1.4
Unidentified hardwood	0	0	0	0	0	0	4	5.6
Total	130	100.0	404	99.9	20	100.0	72	100.1

Tree species choice was significantly related to porcupine age at French Creek ($p<0.001$; $G=35.022$; $df=4$) and at Green Lake ($p<0.005$; $G=27.048$; $df=9$).

MOVEMENTS

The size of winter home ranges and the extent of movements varied greatly among individuals (Table 11). The largest early winter home range was 4422 m^2 (adult female 13, Green Lake) and the smallest range was 9 m^2 (adult female 18, French Creek). In the middle of February most porcupines expanded their home ranges; the largest of these late winter home ranges was 5714 m^2 (adult male 17, French Creek). Home range size was not significantly related to sex, age, or study site.

TABLE 11

Porcupine home range sizes calculated using the minimum convex polygon method

ID #	Sex	Age	Location	Early home range area (m^2) ±5%	Late home range area (m^2) ±5%
4	M	A	Peace Pipe Vista	1,338	-
5	F	J	Green Lake	177	864
7	F	A	Green Lake	288	-
8	M	A	Green Lake	74	2,155
9	F	A	HWY 200	65	-
10	?	?	Ozawindib Trail	1,496	-
11	M	J	French Creek	390	1,468
12	F	A	French Creek	307	1,477
13	F	A	Green Lake	4,422	-
14	F	A	Green Lake	19	-
15	F	A	French Creek	567	1,905
16	F	J	French Creek	19	1,468
17	M	A	French Creek	632	5,714
18	F	A	French Creek	9	1,905
20	?	?	French Creek	-	-

Early winter home range: prior to major range expansions of mid-February.

Late winter home range: after major expansions of mid-February.

In early March a rainstorm resulted in a hard ice crust on top snow that permitted easier travel. During this period, their movements increased greatly with some animals moving into home ranges recently abandoned by others.

Simple correlations were used to determine which factors were related to movement within the home range. Movement was expressed as the linear distance between two consecutive observation points. This gave a conservative

estimate of movement since the distance traveled, as revealed by tracks in the snow, generally was greater than the linear distance. Only observations made on consecutive days were included in the analysis. Linear distance was significantly correlated with sex ($p<0.001$; $r=-0.1832$; point biserial correlation) and maximum wind speed measured at the observation site (Table 12). Mean daily movement of males (21.9 m) was nearly twice that of females (11.6 m). Distance did not correlate significantly ($p<0.05$) with month, ambient temperature, or porcupine age. Daily movement was greatest when windspeeds (measured at observation site) were less than 1.3 m/s. Mean daily movement was less than 12.2 m at windspeeds of 1.3 m/s and greater (Table 12).

TABLE 12

Mean linear distances between observations on consecutive days by maximum windspeed (measured at observation site)

Maximum windspeed m/s	mph	Mean linear distance (m)	N
0	0	17.4	31
0.5	1	19.5	79
0.9	2	14.6	59
1.3	3	5.5	21
1.8	4	7.3	40
2.2	5	11.0	13

($p=0.001$; Pearson's $r=-0.2075$)

SOCIAL ORGANIZATION

The sex ratio was skewed in favor of females (nine females:four males), though not significantly. Most of the porcupines studied were part of two groups resident at French Creek and Green Lake. These groups each consisted of an adult male and a number of females and juveniles. In most cases (78%, N=23), pairs of porcupines sharing feeding trees or dens consisted of an adult female and a juvenile. All juveniles were closely associated with an individual adult female.

BEHAVIORAL THERMOREGULATION

A principal components analysis (varimax rotation) revealed the relationships between the following variables: ambient temperature, maximum wind speed (measured over Lake Itasca), cloud cover, precipitation, tree dbh, height of porcupine in tree, distance from trunk, position relative to trunk and wind direction, and height of lowest branch. Porcupine position relative to trunk and wind direction was expressed as cos(a-b) where a=wind direction and b=direction of trunk relative to porcupine. There were 183 observations which contained values for all of these variables. Three factors were retained (eigenvalues: 2.002, 1.676, 1.379). These factors accounted for 56% of the variance. The correlation matrix is given in Table 13 and the factor pattern is given in Table 14.

TABLE 13

Correlation matrix of behavioral and environmental parameters

	Temp	Wind	Clcr	Prec	DBH	Hght	Dist	Angl
Wind	0.076	-	-	-	-	-	-	-
Clcr	0.268	0.282	-	-	-	-	-	-
Prec	-0.183	0.267	0.402	-	-	-	-	-
DBH	0.143	0.010	-0.009	0.012	-	-	-	-
Hght	0.324	-0.077	0.128	-0.061	0.434	-	-	-
Dist	-0.152	0.013	-0.117	0.043	0.182	0.128	-	-
Angl	0.079	-0.093	-0.056	-0.130	-0.111	0.037	-0.116	-
Brht	0.365	-0.010	0.053	-0.043	0.278	0.337	-0.104	0.026

Temp=ambient temperature, Wind=maximum wind speed, Clcr=cloud cover, Prec=precipitation, Hght=porcupine height, Dist=distance from trunk, Angl=position relative to trunk and wind direction

TABLE 14

Factor pattern for principal component analysis of behavioral and environmental parameters (varimax rotation)

	Factor 1	Factor 2	Factor 3
Ambient temperature	0.673	0.117	-0.418
Maximum wind speed	-0.022	0.663	0.030
Cloud cover	0.208	0.780	-0.186
Precipitation	-0.150	0.737	0.236
DBH	0.626	-0.035	0.494
Porcupine height	0.772	-0.048	0.197
Distance from trunk	0.012	-0.101	0.751
Position relative to trunk and wind direction	0.046	-0.249	-0.497
Height of lowest branch	0.699	-0.003	-0.143

Ambient temperature, dbh, porcupine height, and height

of lowest branch loaded high on factor 1. Maximum wind speed, cloud cover, and precipitation loaded high on factor 2. Ambient temperature, dbh, distance from trunk, and position relative to trunk and wind direction loaded high on factor 3. Ambient temperature and position relative to trunk and wind direction were negatively correlated with factor 3.

The relationships between ambient temperature and tree choice and between tree type and height of lowest branch were investigated further. Porcupines were found in hardwoods or dens (only three animals utilized dens) more frequently at lower temperatures than at higher temperatures (Figure 2). Porcupines chose lower positions in trees at lower temperatures ($p<0.001$; Pearson's $r=0.37129$; $N=541$). The height of the lowest branch was lower in hardwoods than in conifers (Table 15). The mean dbh of hardwoods (31.0 cm) was significantly smaller than the mean dbh of conifers (51.6 cm) ($p<0.001$; $t=3.653$, $df=707$).

Ambient and den temperatures were recorded simultaneously at two dens: one used by porcupine 4 and one shared by porcupines 5 and 7. Mean den temperature (-9.6 ^{o}C) was significantly higher than mean ambient temperature (-16.2^{o}C) for both dens pooled ($p<0.001$; $t=3.960$; $df=34$). There were no significant differences in ambient or den temperatures between dens. The den shared by

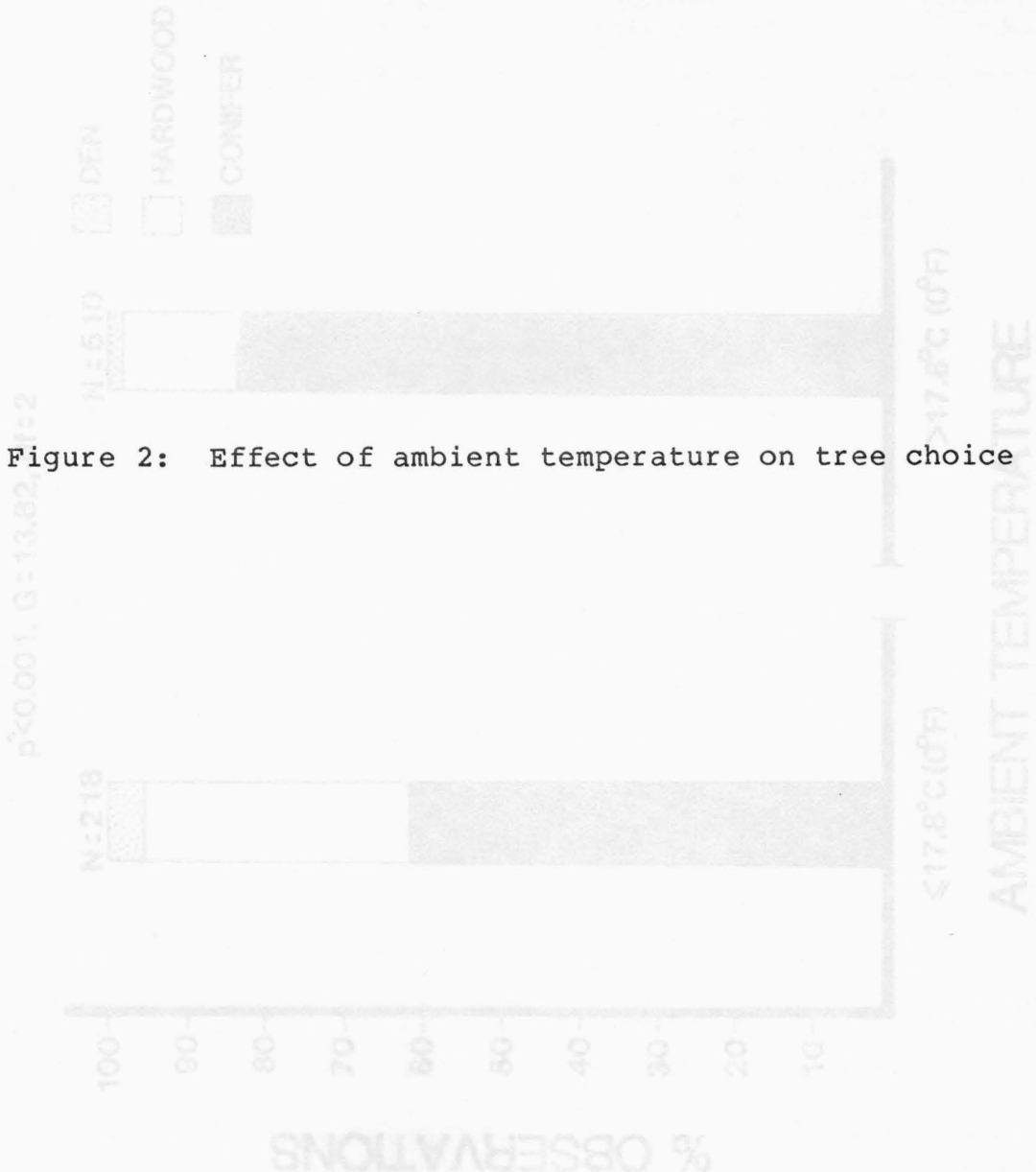


Figure 2: Effect of ambient temperature on tree choice

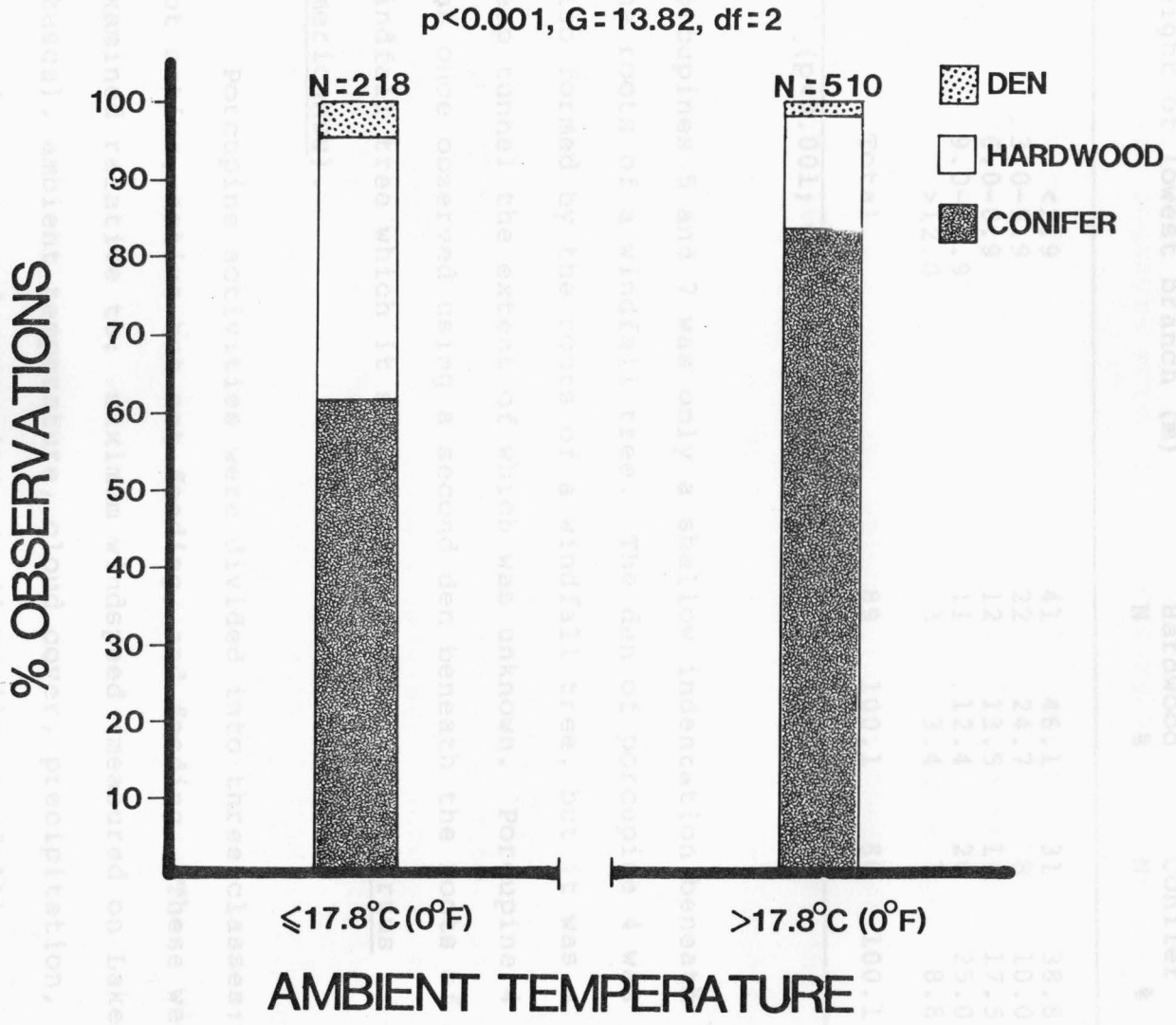

p<0.001, G=13.82, df=2
N=218
N=510
DEN
HARDWOOD
CONIFER
100
90
80
70
60
50
40
30
20
10
% OBSERVATIONS
≤17.8°C (0°F)
>17.8°C (0°F)
AMBIENT TEMPERATURE

TABLE 15

Relationship between tree type and height of lowest branch

Height of lowest branch (m)	Hardwood N	Hardwood %	Conifer N	Conifer %
<2.9	41	46.1	31	38.8
3.0-5.9	22	24.7	8	10.0
6.0-8.9	12	13.5	14	17.5
9.0-11.9	11	12.4	20	25.0
>12.0	3	3.4	7	8.8
Total	89	100.1	80	100.1

($p<0.001$; $G=20.994$; $df=4$).

porcupines 5 and 7 was only a shallow indentation beneath the roots of a windfall tree. The den of porcupine 4 was also formed by the roots of a windfall tree, but it was a deep tunnel the extent of which was unknown. Porcupine 4 was once observed using a second den beneath the roots of a windfall tree which it shared with a black bear (Ursus americanus).

Porcupine activities were divided into three classes: not active, active but not feeding, and feeding. These were examined relative to: maximum windspeed (measured on Lake Itasca), ambient temperature, cloud cover, precipitation, porcupine sex, and porcupine age (juvenile or adult). Activity class was significantly related to ambient temperature ($p<0.001$; $F=2.24$; $df=50$) and sex of porcupine

(Figure 3). During daylight hours, porcupines fed at lower temperatures (-5.5 ^{o}C) than when active but not feeding (-4.6 ^{o}C), or when inactive (-3.7 ^{o}C) ($p<0.001$; $F=2.24$; $df=50$). Males were more active than females and feeding was observed more often among males than females.

Analyses of variance were used to determine which aspects of spatial position were related to activity class. Aspects of position investigated included: tree species (only those tree species for which activity observations were available were used), dbh, distance from trunk, and height in tree. Tree species was significantly related to porcupine activity (Table 16).

Activity class was significantly related ($p<0.01$) to the following tree species (Table 17): white pine, red oak, and balsam fir. The relationship between activity class and American basswood was significant ($p=0.05$). Porcupines were inactive during more than 60% of the observations in the following tree species: white pine, bigtooth aspen, and American elm. The percentage of observations during which porcupines were active but not feeding was comparable, ranging from 6.2% for white pine to 28.6% for white spruce (or 15.0% for balsam fir). The largest percentages of observations of porcupines feeding were 45.0% for balsam fir, 40.9% for red oak, and 37.5% for American basswood (Table 17).

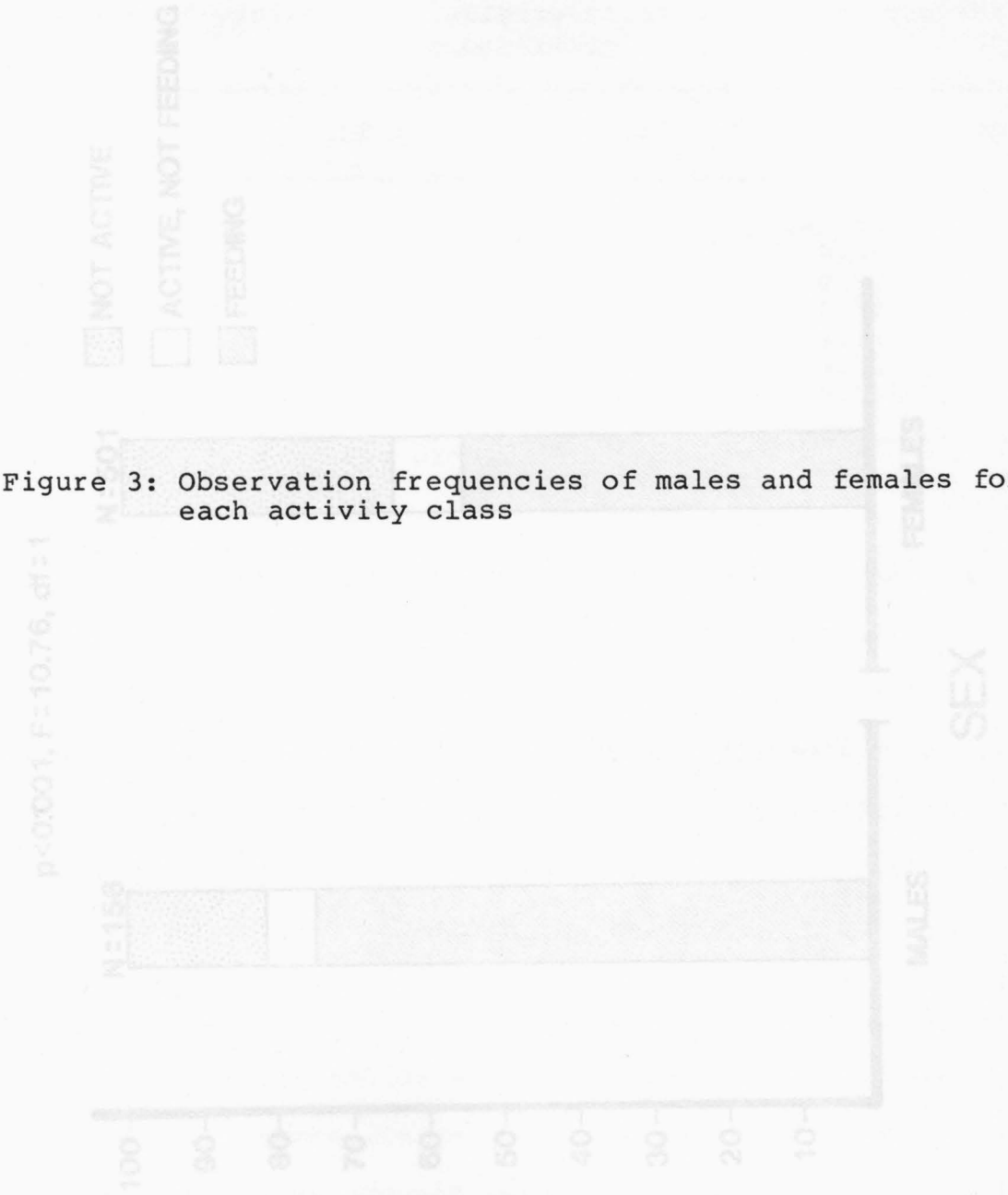
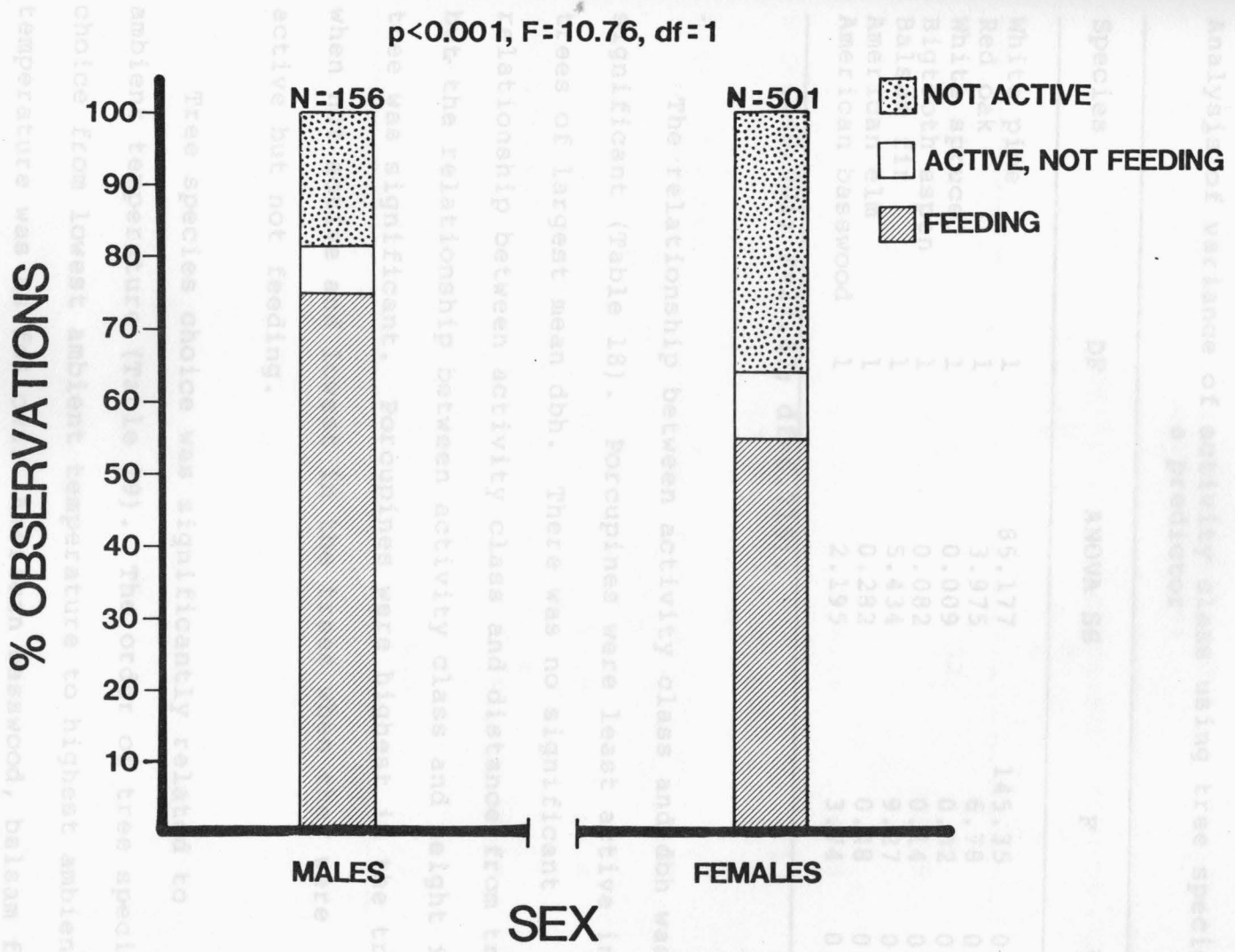


Figure 3: Observation frequencies of males and females for each activity class


p<0.001, F=10.76, df=1
N=156
N=501
NOT ACTIVE
ACTIVE, NOT FEEDING
FEEDING
% OBSERVATIONS
100
90
80
70
60
50
40
30
20
10
MALES
FEMALES
SEX

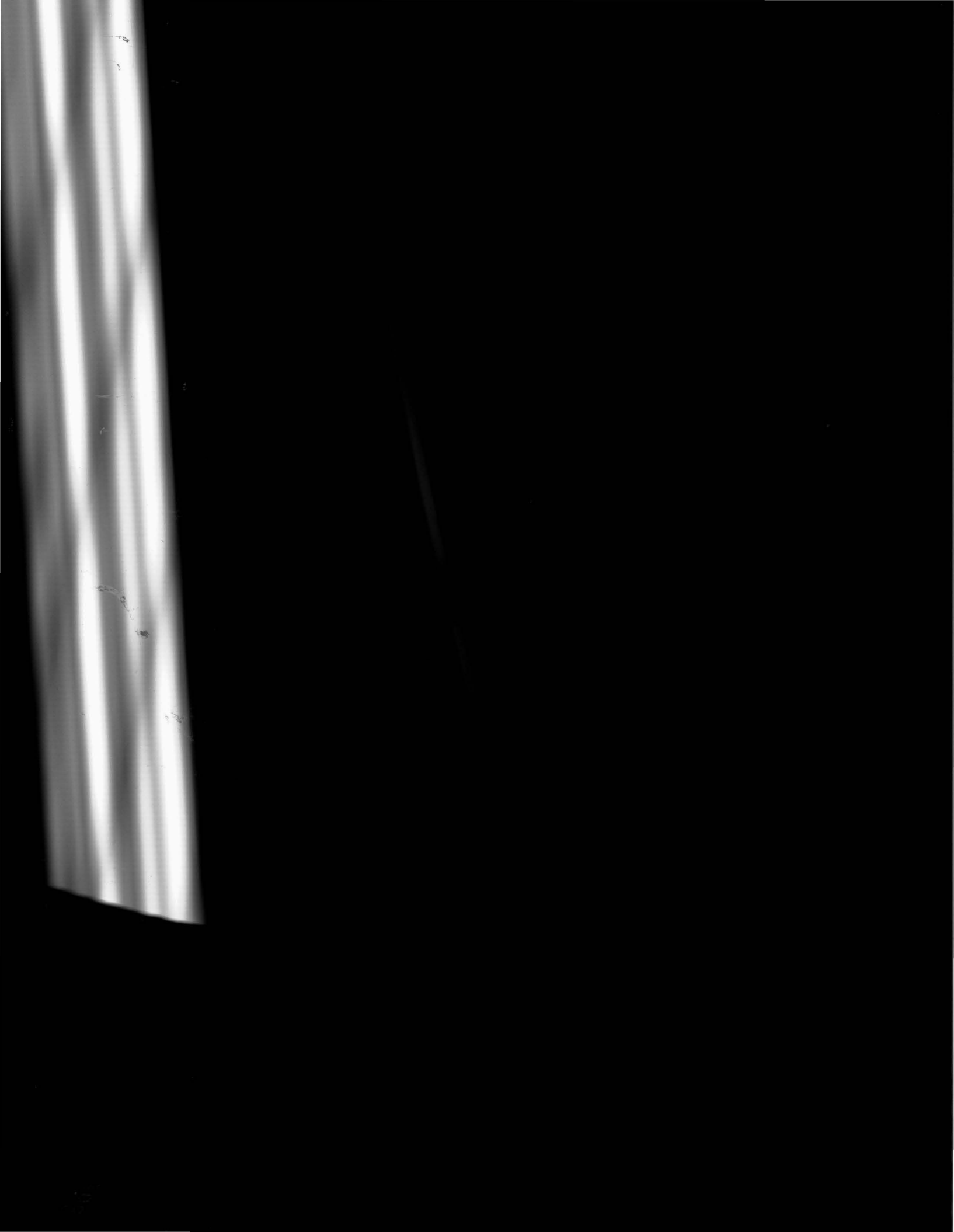


TABLE 16

Analysis of variance of activity class using tree species as a predictor

Species	DF	ANOVA SS	F	PR>F
White pine	1	85.177	145.35	0.0001
Red oak	1	3.975	6.78	0.0094
White spruce	1	0.009	0.02	0.9021
Bigtooth aspen	1	0.082	0.14	0.7092
Balsam fir	1	5.434	9.27	0.0024
American elm	1	0.282	0.48	0.4878
American basswood	1	2.195	3.74	0.0534

($p<0.001$; $F=27.67$; $df=6.715$).

The relationship between activity class and dbh was significant (Table 18). Porcupines were least active in trees of largest mean dbh. There was no significant relationship between activity class and distance from trunk, but the relationship between activity class and height in tree was significant. Porcupines were highest in the trees when not active and lowest in the trees when they were active but not feeding.

Tree species choice was significantly related to ambient temperature (Table 19). The order of tree species choice from lowest ambient temperature to highest ambient temperature was as follows: American basswood, balsam fir, white pine, white spruce, and American elm. Due to small sample size of temperature recordings at Green Lake, only French Creek temperatures were subjected to analysis.

TABLE 17

Frequencies of observations of utilized tree species of each activity class

Species	Not Active N %	Active,Not Feeding N %	Total N %
White pine	419 80.9	32 6.2	67 12.9	518 100.0
Red oak	10 45.5	3 13.6	9 40.9	22 100.0
White spruce	4 57.1	2 28.6	1 14.3	7 100.0
Bigtooth aspen	5 71.4	1 14.3	1 14.3	7 100.0
Balsam fir	8 40.0	3 15.0	9 45.0	20 100.0
American elm	28 63.6	5 11.4	11 25.0	44 100.0
American basswood	13 54.2	2 8.3	9 37.5	24 100.0

TABLE 18

Mean values of dbh, distance from trunk, and height in tree for each activity class

	Not active	Active, not feeding	Feeding
Mean dbh in cm	51.1	49.3	42.2
(N)	(488)	(48)	(109)
Mean distance from trunk in m	1.3	1.7	1.3
(N)	(405)	(25)	(65)
Mean height in tree in m	15.4	13.8	14.4
(N)	(442)	(31)	(75)

Activity class significantly related to dbh ($p<0.001$; $F=25.51$; $df=1, 643$).

Activity class significantly related to height ($p=0.05$; $F=3.87$; $df=1, 546$).

TABLE 19

Mean ambient temperatures by tree species and study area

Tree species	Mean ambient temperature			
	French Creek		Green Lake	
	C	N	C	N
White pine	-1.6	402	-14.2	49
Red oak	-	-	-14.6	16
White spruce	-0.7	3	-5.6	1
Bigtooth aspen	-	-	-13.4	4
Balsam fir	-8.2	12	-	-
American elm	0.4	35	-	-
Bur oak	-	-	-6.1	1
American basswood	-11.5	11	-12.9	8
Red pine	-	-	-6.8	3
Unidentified hardwood	-	-	-7.2	2
Total	-	463	-	84

($p<0.001$; $F=10.16$; $df=4, 458$).

DISCUSSION

FOOD AND HABITAT PREFERENCES

Foraging efficiency increases when an animal selects food in such a manner that energy gained from the food is maximized while energy used to search for, handle, and process it is minimized. In addition to maintaining a positive energy balance, an animal must fulfill specific nutritional needs (e.g. minerals, vitamins). If diet selection is dominated by the need to meet nutritional criteria, then the relationship between utilization of particular foods and availability should not be continuous. Necessary foods would be included in the diet until a cutoff is reached at a very low availability, after which the food would no longer be included in the diet (Westoby 1974). This implies that foraging pressure on a given plant species will increase as availability decreases until the cutoff is reached. Therefore, if a food is to be preferred, it must either be readily available (Morse 1980) or contain some necessary nutrient not readily available in a more common species.

Porcupine food preferences vary tremendously across the species range. Some of the winter preferences recorded

include: douglas fir (Pseudotsuga menziesii), limber pine (Pinus flexilis), and hybrid spruce (Picea glauca X Picea engelmannii) in southwestern Alberta (Harder 1980); white pine (Pinus strobus), eastern larch (Larix laricina), and gray birch (Betula populifolia) in New Brunswick (Speer and Dilworth 1978); eastern hemlock (Tsuga canadensis) in upper Michigan (Brander 1973); limber pine in southern Alberta (Gill and Cordes 1972); sugar maple (Acer saccharum), beech (Fagus grandifolia), yellow birch (Betula lutea), white birch (Betula papyrifera), white pine, and white spruce (Picea glauca) in New England (Faulkner and Dodge 1962); sugar maple, American basswood (Tilia americana), yellow birch, black cherry (Prunus serotina), eastern hemlock, tamarack (Larix laricina), jack pine (Pinus banksiana), white pine, and red pine (Pinus resinosa) in the lake states (Krefting et al. 1962); ponderosa pine (Pinus ponderosa) in South Dakota (Van Deusen and Myers 1962); eastern hemlock, red spruce (Picea rubens), and sugar maple in Maine (Curtis and Kozicky 1944); yellow pine (Pinus ponderosa), douglas fir, and spruce (Picea sp.) in Oregon (Gabrielson 1928); spruce and white birch in Alaska (Murie 1926). Clearly, evaluation of food preference is useful only when taken in the context of species presence and abundance.

Tree species compositions at the two study sites were significantly different. There was a greater abundance and diversity of conifers at French Creek than at Green Lake.

Tree species preferences were determined in two ways: by porcupine observation frequencies and by new bark damage. White pine was preferred over all other available species at both sites and preferences were also shown for American elm and American basswood at French Creek, and for bigtooth aspen and red oak at Green Lake based on observation frequencies and new bark damage. In addition, preferences were shown for balsam fir at French Creek and American basswood at Green Lake based on observation frequencies alone. Apparently these species were not used mainly for bark forage, but served as places of rest, shelter, and in the case of balsam fir, needle forage. Juveniles and females were observed in conifers more often than males, possibly indicating a higher nutritional value of conifer bark and needles. Dependence upon needles for food was greater at French Creek where conifers were more abundant.

Tree species with abundances of less than 1% were not utilized. In no case did the proportion of damaged trees increase with decreasing abundance. This indicates that necessary nutrients could be found in a variety of species. Thus, where certain species were rare or absent, other more abundant species were utilized instead.

Although white pine was the most important species for porcupines in this study, it is unlikely that there is a "universal food of porcupines" as Murie (1926) suggested.

Preferences are influenced by availability, thus Hansen et al. (1974) reported a feeding preference for red pine in Itasca Park- in an area where that species was the dominant overstory species.

Porcupines have been reported to show winter preferences for large dbh trees: 9-15 inches (22.9-38.1 cm) in the the lake states (Krefting et al. 1962); greater than 7 inches (17.8 cm) in northern Minnesota (Marshall et al. 1962); 6-7.9 inches (15.2-20.1 cm) in South Dakota (Van Deusen and Myers 1962); and 3.9 inches (9.9 cm) in lake states pine plantations (Rudolf 1949).

French Creek porcupines preferred trees greater than 15.0 cm dbh while Green Lake animals preferred trees greater than 30.0 cm dbh. This reflected the greater abundance of large dbh trees at Green Lake. Larger trees may be preferred because they are easier to climb, more stable in strong winds, or their branches are larger and provide better resting places. Larger trees also may offer better concealment against predators.

If an environment is patchy with respect to food resources, patches utilized by an animal are expected to contain a greater abundance of foods important to that animal. When areas utilized by porcupines were compared with unutilized areas nearby, differences in species and dbh composition were found. White pine was more abundant in

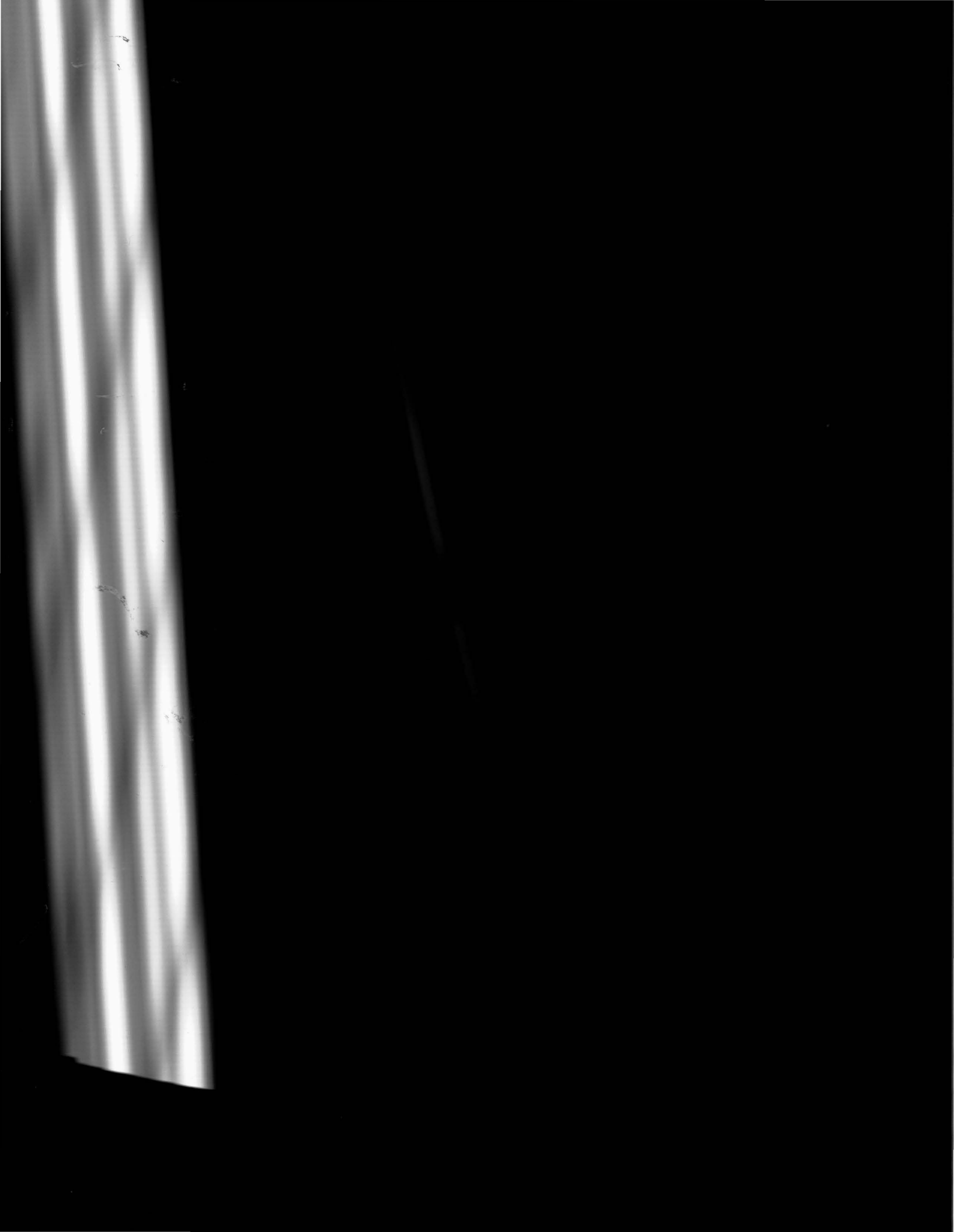
utilized areas and there was more red oak in unutilized areas at Green Lake. Apparently white pine was more important to porcupines than red oak in determining home range placement. Utilized areas had larger proportions of large dbh trees. Tree density was uniform for all areas examined and therefore was not a determinant of habitat preference.

The fate of the white pine in Itasca Park is uncertain. Of the 31,586 acres (12,782 ha) included in the park, only 847 acres (343 ha) are predominantly white pine as compared to 5,738 acres (2,322 ha) of red pine (Hansen et al. 1974). The porcupines damaged between 40% and 70% of the number of white pine available within their winter home ranges. In order to understand the implications of porcupine damage to the future of the Itasca white pine, a number of other factors need to be taken into account, such as the age composition of present white pine stands. Of the 847 acres of white pine, 739 acres (299 ha) consist of overmature trees (over 200 years old with an average life expectancy of about 25 years) and the remaining 108 acres (44 ha) consist of mature white pine (90 to 150 years old). Reproduction of all pines is sparse and is concentrated on dry, nutrient-poor sites under predominantly jack pine cover (Hansen et al. 1974).

Porcupine damage to white pine is mainly restricted to mature trees. The future of white pine in Itasca Park depends on regeneration. In 1920, white pine blister rust (Cronartium ribicola) was a sufficient threat to white pine plantings to warrant an eradication program of the alternate host, Ribes, within Itasca Park (Hansen et al. 1974). There are a number of mammals in the park that depend on woody browse for winter food, including cottontail rabbits (Sylvilagus floridanus), snowshoe hare (Lepus americanus), gray squirrel (Sciurus carolinensis), fox squirrel (Sciurus niger), whitetail deer (Odocoileus virginianus), and moose (Alces alces). These species are probably a greater threat to white pine regeneration than are porcupines. Spurr and Barnes (1980) stated that causes for seedling damage included clipping and bark removal by hares; stem and root girdling by voles, mice, shrews, and pocket gophers; and trampling and browsing by deer. Perhaps exclosures in white pine stands would facilitate regeneration. It seems doubtful that porcupine control would remedy the situation.

MOVEMENTS

Like food preferences, home range sizes vary greatly from place to place. Faulkner and Dodge (1962) reported a winter home range size in New England of 6 acres (2.4 ha). Smith (1979) reported home range areas in northeastern Oregon of 3.9 ha for a male in January and 8.1 ha for a



female in February and March. These areas were 4-14 times larger than those in Itasca Park. Porcupine home range sizes in Itasca Park varied between 9 m^2 and 5,714 m^2 (0.5714 ha). These regional differences were probably due to differences in habitat quality. Brander (1973) stated that winter travel was dependent upon locations of feeding trees and dens. There are almost certainly regional differences in suitable feeding tree and den densities.

Linear distance traveled was significantly related to sex and maximum windspeed (measured at observation site), but not to month, ambient temperature, or age. Mean daily movement of males was nearly twice that of females. Mean daily movement was less than 12 m at wind speeds of 1.3 m/s and greater. Porcupines have a poor sense of vision (Spencer 1950) and probably depend largely on hearing for predator detection. On windy days it is more difficult to hear the approach of another animal, thus porcupines may avoid being on the ground on windy days in order to avoid potential predators.

SOCIAL ORGANIZATION

Little work has been done on porcupine mating systems. Struthers (1928) stated that males probably mate with a single female, although some males probably mate twice. Curtis (1941) also reported monogamy in porcupines. But unequal sex ratios skewed in favor of females have also been reported by several investigators (Struthers 1928; Brander 1973; Smith 1977). The clumped groups of porcupines at French Creek and Green Lake each consisted of one adult male and a number of females and juveniles. It seems plausible that these clumps may represent family groups, each consisting of a male and his mates plus offspring. Porcupines mate in fall, and it appears that a male and his mates overwinter together. If breeding does not occur, repetition of the estrus cycle every 25 to 30 days extends late into January (Faulkner and Dodge 1962).

The young are born in the spring and have been reported to remain with their mothers throughout the summer (Marshall et al. 1962). All three of the juveniles observed were closely associated with an individual female, sharing dens and feeding trees. As spring neared, females became less closely associated with their offspring. In one instance in the middle of February an agonistic encounter between an adult female and her offspring lasted about three hours. During this encounter the juvenile followed and harassed the female who retaliated by snapping at it.

The clumping of porcupines in closely associated home ranges affects tree damage distribution, but probably does not affect degree of damage since home ranges rarely overlapped except in cases of mother-offspring pairs.

BEHAVIORAL THERMOREGULATION

In order for an animal to survive in a cold environment, a balance must be reached between heat production and heat loss. Heat loss may be minimized by insulation (e.g. pellage and subcutaneous fat), vasoconstriction, counter-current heat exchange, and by behavioral means such as sunning and seeking shelter from the wind. Heat production may be maximized by motor activity, shivering, imperceptible tensing of muscles, chemical increase of metabolic rate (e.g. via norepinephrine), specific dynamic action of food, and fever (Folk 1966). Heat production requires energy and thus food availability is an important limiting factor for survival in a cold environment. Morrison (in Folk 1966) stated that 'Animals with adequate food either in stores or accessible in the environment need not fast. Fasting (and hibernation) is only found in animals with inadequate external food reserves, whatever the reason. Animals without external food reserves must use internal reserves and often hibernate.'

Porcupines in Itasca Park utilize a food resource (inner cambium layer two meters or greater above the ground) with little potential competition from other species. Gray squirrel and fox squirrel may feed on inner cambium in the winter, but their winter staple food is seeds (Smith and Follmer 1972). Two other rodents of size comparable to the porcupine occur in Itasca Park: woodchuck (Marmota monax) and beaver (Castor canadensis). Each of these animals deal with the problem of a cold environment in a different fashion. Woodchucks hibernate. Beavers cache food, store fat deposits, and are never active above ice when the ambient temperature drops below -10°C (Lancia et al. 1982). Most smaller mammals either hibernate (e.g. ground squirrels, Spermophilus sp.; chipmunks, Tamias sp. and Eutamias sp.) or find shelter in tunnels in the snow (e.g. red squirrel, Tamiasciurus hudsonicus). A few of the larger carnivores experience winter lethargy: striped skunk (Mephitis mephitis), badger (Taxidea taxus), raccoon (Procyon lotor), and black bear (Ursus americana) (Folk 1966). The remaining larger mammals at Itasca Park- whitetail deer, moose, mustelids other than skunk and badger (Family Mustelidae), felids (Family Felidae), canids (Family Canidae), cottontail rabbit, and snowshoe hare - are active throughout the winter. Body mass alone does not seem to be the primary determinant of winter activity, although it may restrict some types of activity (e.g. snow tunnels).

Overall energy balance is a more important determinant of winter activity patterns.

In order to exploit the inner cambium food resource in the treetops, porcupines must be exposed to harsh winter conditions. Moen (1968) pointed out that factors other than air temperature (e.g. wind speed, cloud cover, body size, and posture) play an important role in determining an animal's thermal environment.

An hypothesis was formulated to predict porcupine behavior relative to the thermal environment. Stated simply, porcupines were expected to choose more sheltered positions under unfavorable weather conditions. Unfavorable weather conditions were subjectively defined to include cold temperatures, high wind speeds, maximal cloud cover, and maximal precipitation. Sheltered positions were subjectively defined to include dens and conifers with large diameters, leeward positions near trunk, and positions nearer to ground. Lower positions in trees were expected to be more favorable for two reasons: windspeed decreases with decreasing height due to wind shear, and temperature increases with decreasing height during the day due to convection currents produced as the ground heats (Anthes et al. 1981). When weather conditions were favorable, porcupines were expected to choose positions in a more random fashion.

To minimize thermal stress, behavioral means of thermoregulation were utilized. Although den temperatures were much warmer than ambient temperatures, porcupines were found in dens only when temperatures dropped below -9°C. Even at temperatures below -18°C, porcupines were found in dens only five percent of the time. Based on tracks, most porcupines did not have dens. This conflicts with the earlier report that porcupines in Maine rarely leave their dens when the air temperature is below 0°F (-17.8°C) (Curtis and Kozicky 1944). There are a variety of potential explanations for this discrepancy. The humidity may have been greater in Maine than in Minnesota, resulting in a greater heat loss problem. Suitable dens near feeding trees may have been more plentiful in Maine. Porcupines in Maine may have needed to stay in dens to maintain a positive energy balance if food was scarce or of poor quality.

Porcupines fed and were more active when ambient temperatures were lower. Feeding and motor activity may act as mechanisms of behavioral thermoregulation. Both increase heat production over basal metabolic rate (Folk 1966). According to W.D. Schmid (pers. commun.), porcupine winter body temperatures were relatively constant (approximately 36.6°C) throughout the day and night when the animals were in the trees, regardless of whether they were active or inactive. This indicates that they were maintaining a balance between heat production and heat loss. When in

dens, their body temperatures were lower (approximately 35.6°C) than when in trees (Schmid, pers. commun.). Porcupines may eat snow in their dens to combat dehydration, causing a decrease in body temperature.

Porcupines were found in trees of smaller dbh and at lower heights, when feeding and active because hardwoods of relatively small dbh had lower first branch heights, permitting lower porcupine positions. Height and dbh choice were apparently more strongly related to ambient temperature than to feeding preferences (porcupines prefer larger dbh trees based on new bark damage observations). The shelter provided by lower positions in terms of less wind and possibly higher temperatures apparently outweighed the shelter value of conifer foliage and large trunks, contrary to the initial predictions. These two strategies are mutually exclusive.

Porcupines were least active during daylight hours in white pine and American elm, while spending the most time feeding in balsam fir, red oak, and American basswood. At French Creek, the mean ambient temperature for porcupine observations in white pine and American elm was above -2°C. The mean ambient temperature for balsam fir and American basswood was below -8°C. Presumably, these species offered more shelter than species associated with higher ambient temperatures. At lower ambient temperatures,

porcupines would be expected to choose sheltered positions, and feeding and activity would be advantage for staying warm. Males were more active and fed more frequently than females, possibly due to differences in basal metabolic rate or insulation.

CONCLUSIONS

The French Creek and Green Lake habitats were significantly different in tree dbh and tree species composition, but not in tree density. Conifers were more abundant at French Creek. Sham home ranges scattered randomly among actual home ranges revealed that the actual home ranges at both study sites were chosen because of desirable characteristics such as relatively high proportions of large dbh trees and white pines. Tree density was not an important factor in home range selection.

Bark food preferences were determined by comparing new bark damaged trees with the total trees available within the home ranges. The preferred species were dependent on species composition and thus there were differences between French Creek and Green Lake in species preferences. Preferred species at French Creek included white pine, American elm, and American basswood. Preferred species at Green Lake included white pine, bigtooth aspen, and red oak. Porcupine observation frequencies corresponded relatively well with species preferences calculated from new bark damage frequencies.

Porcupines at French Creek depended on needles more than on bark for food, but the reverse was true at Green Lake, reflecting the greater abundance of conifers at French Creek. French Creek females and juveniles utilized more conifers than males, possibly for nutritional reasons.

White pine was the most important winter species utilized by porcupines in this study. However, importance of tree species to porcupines is largely dependent on tree species availability and should not be generalized without some caution. White pine is relatively scarce in Itasca Park and consists mostly of overmature trees. Forest management should be aimed at maximizing white pine reproduction. Since porcupines feed largely on mature trees, control measures (e.g. exclosures in selected areas) should be utilized for animal species that damage the seed crop and seedlings.

Daily movements within home ranges were related to porcupine sex and maximum wind speed (measured at the observation site). Males traveled nearly twice as far as females daily. Travel was restricted on windy days, possibly because of increased vulnerability due to difficult predator detection.

Each of the two groups studied (French Creek and Green Lake) consisted of a single adult male and a number of females and juveniles. It was postulated that these were

family groups. After mating in fall, the male apparently overwinters with his mates. All three juveniles were closely associated with individual adult females. This association probably ceases in early spring as the time of parturition nears.

Porcupines used a variety of behavioral means of thermoregulation. At lower temperatures they sought shelter by choosing positions closer to the ground. Because hardwoods of relatively small dbh had lower first branch heights permitting lower porcupine positions, these factors also were related to lower temperatures. The shelter provided by lower positions in terms of less wind and possibly higher temperatures outweighed the shelter value of conifer foliage and large trunks. These two strategies were mutually exclusive. Porcupines were more active and fed more frequently at lower temperatures, thus increasing their heat production. The major determinant of thermal environment of porcupines appeared to be ambient temperature. Porcupine den temperatures were significantly higher than ambient temperatures, but dens were only used when ambient temperatures dropped below $-9^{\circ}C$. Most porcupines lacked dens.

In conclusion, porcupines are well-adapted to stay active throughout harsh winters. They maintain a positive energy balance by utilizing a resource, inner cambium of

treetops, with little competition from other animals. They also utilize behavioral means of thermoregulation. Most of the porcupines of this study belonged to two groups, each consisting of a male and a number of females and young. It was postulated that this was a male, his mates, and offspring. Foraging behavior was also investigated and the preferred tree species was white pine. It was suggested that porcupines are not a major threat to white pine because they prefer mature trees. The future of the white pine in Itasca State Park appears to depend upon adequate protection of the seed crop and seedlings rather than the older trees.

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